ZOOLOGICAL SCIENCE 5: 299–309 (1988)

The Anatomy and Physiology of the Stomatogastric Nervous System of *Squilla*. II. The Cardiac System

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ABSTRACT—A subsystem of the stomatogastric ganglion (STG) of the mantis shrimp, *Squilla oratoria*, which controls movements of the cardiac stomach was studied. Muscles of the cardiac stomach and their motor nerves leaving the STG are described. The paired anterior ventricular nerves and paired lateral ventricular nerves (lvn), which exit the STG, contain the motor axons that control muscular contractions of the cardiac stomach. One pair of superior oesophageal nerves (son) also carry motor axons. The lvn and son give rise to several peripheral nerves which innervate 8 identified muscles. Spontaneous motor activity recorded from the lvn and son (termed the cardiac cycle) has a long cycle period (ca. 10 sec) and consists of alternate firing of bursts by two motor neuron groups. Cardiac cycles similar to spontaneous ones are triggered by stimulation of afferent fibers entering the commissural ganglia. Four constrictor and 3 dilator motor neurons in the STG are identified. They are involved in sequential movements of the dorsal and lateral gastric walls of the cardiac stomach. The function of the cardiac cycle is described with reference to the maceration and transfer of food. It is compared to that of the posterior cardiac plate and pyloric cycle (pcp-pyloric cycle) which has been described previously. Comparisons are made of the cardiac systems in STG of stomatopods and decapods.

INTRODUCTION

The stomatogastric ganglion (STG) of decapods, a small, semi-autonomous nervous system, has been extensively studied as a model for the generation of patterned motor outputs [1, 2]. In the STG both individual cellular properties and neural networks can be analyzed. The lobster STG contains just over 25 identifiable motor neurons which innervate identified muscles of the cardiac and pyloric stomachs [3–5]. It produces cyclic patterned motor outputs having two distinct rhythms responsible for the sequential muscular contractions of the gastric and pyloric regions of the stomach, respectively [6, 7]. The gastric and pyloric cycles are modulated by the supra-oesophageal and commissural ganglia (CG) [8–10]. The cardiac dilator and constrictor neurons are identified in the lobster STG and oesophageal ganglion (OG), and their motor activity modulates the pyloric cycle or coordinates it with the gastric cycle [11, 12].

The stomach in stomatopods is subdivided into the cardiac stomach, the posterior cardiac plate (pcp) and the pyloric stomach [14, 15]. The cardiac stomach is not equipped with a chewing apparatus such as the gastric mill ossicles of decapods. Most of the ossicles of the stomach form the pcp and pyloric systems of sieves and channels through which digested food moves. The muscles in the stomach and their sequential movements have been described by Kunze [15].

The anatomy and physiology of the stomatogastric nervous system of *Squilla* have been found to be similar to those of decapods [16]. Its gross anatomy was first described by Police [13]. The stomatogastric nervous system in stomatopods is basically similar to that in decapods. While the STG in decapods sends several unpaired and paired motor nerves to control the gastric mill and pyloric stomach, the paired lateral ventricular nerves (lvn) which leave the STG in stomatopods carry principal motor axons to innervate the

Accepted August 26, 1987
Received May 22, 1987

muscles of the pcp and pyloric stomach. Characteristics of the cyclic motor outputs observed in the lvn have been described previously in relation to the channel-opening function of the pcp and pyloric systems. The patterned motor outputs have been termed the pcp-pyloric cycle. The pcp-pyloric cycle of stomatopods is apparently homologous to the pyloric cycle in decapods although the neural circuits for its pattern generation remain to be analyzed. The pcp-pyloric cycle is also modulated by input fibers of the superior and inferior oesophageal nerves (son, ion). Cardiac motor activity controlling movements of the cardiac stomach is rarely observed to occur spontaneously in the semi-isolated preparation, but can be triggered or primed by stimulation of the son input fibers.

The present paper deals with the anatomy and physiology of the cardiac system of the stomatogastric nervous system of the mantis shrimp, *Squilla oratoria*. Muscles of the cardiac stomach and their motor nerves are described. The cyclic motor activity of the STG is shown to explain the sequential muscular contractions which control the functional movements of the cardiac stomach. Relations between the cardiac and pcp-pyloric systems primed by stimulation of the son are analyzed.

MATERIALS AND METHODS

The stomatogastric nervous system of a stomatopod, *Squilla oratoria*, was employed in this study. Animals were held in tanks of recirculated sea water at the temperature of 20°C. About 200 specimens were used for anatomical and physiological observations. Methods of dissection and recording were the same as those described in the previous paper [16].

Cardiac stomach

The cardiac stomach, which is a large cuticular sac serving to store ingested food, contains two pairs of ossicles [15]. The anteroventral cardiac ossicles (avc) lie along the anterior lateral margins of the ventral gastric wall (Fig. 1A). They act as supports for muscle attachment. The small posterior lateral cardiac ossicles lie in the posterior

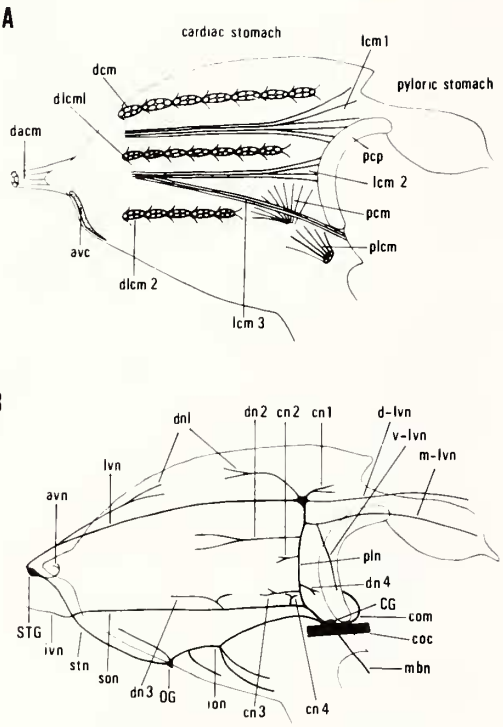

FIG. 1. A: Diagrammatic lateral view of musculature in the cardiac stomach. avc, anteroventral cardiac ossicle: pcp, posterior cardiac plate: dacm, dorsal anterior cardiac muscle: dcm, dorsal cardiac muscle: dlcm1 and dlcm2, dorsolateral cardiac muscle: lcm1–lcm3, longitudinal cardiac muscle: pcm, posterior cardiac muscle: plcm, posterior lateral cardiac muscle.

B: Diagrammatic lateral view of the stomatogastric nervous system. The diagram shows peripheral nerve courses of the lvn and son. CG, commissural ganglion: OG, oesophageal ganglion: STG, stomatogastric ganglion: coc, circumoesophageal connective: com, commissure: ion, inferior oesophageal nerve: ivn, inferior ventricular nerve: mbn, mandibular nerve: son, superior oesophageal nerve: stn, stomatogastric nerve: avn, anterior ventricular nerve: lvn, lateral ventricular nerve: d–lvn, dorsal lateral ventricular nerve: m–lvn, median lateral ventricular nerve: v–lvn, ventral lateral ventricular nerve: pln, posterior lateral nerve: cn1–cn4, cardiac constrictor nerve: dn1–dn4, cardiac dilator nerve.

lateral gastric wall anterior to the pcp (not shown), though their function is unknown. These two ossicles do not play a role of masticating ingested food. Kunze [15] has classified the muscles in the cardiac stomach into three groups: cardiac mus-

cles, longitudinal muscles and cardiac floor muscles. All of these muscles have been named, and the sequence of movements of the cardiac stomach after ingestion has been described. However, the functional anatomy of the muscles of the cardiac stomach has not been described in detail, and their origins and insertions remain obscure. The stomach muscles are divided into two groups: extrinsic muscles originating on the inner side of the exoskeleton and inserting on the stomach wall or ossicles, and intrinsic muscles having both attachments on the stomach wall itself [5]. Contractions of these individual muscles constrict or dilate different regions of the gastric wall. In this paper, the muscles in the cardiac stomach, which are innervated by motor nerves leaving the STG, have been identified (see *Anatomy* section).

Preparation

Two types of preparations were used in this study. The semi-intact preparation was made in order to record the spontaneous cardiac motor activity. After cutting away most of the appendages in the cephalothoracic region, the animal was immobilized, ventral side up, in the preparation box filled with saline. The ventral and lateral regions of carapace anterior to the mandibles were removed by cutting the extrinsic muscles thus exposing the cardiac stomach and the stomatogastric nervous system. The cardiac stomach moved rhythmically for two hours or more under these conditions. The lvn and son, which include motor axons controlling movements of the cardiac stomach, were drawn into suction electrodes. This preparation was also used to observe how the extrinsic and intrinsic muscles move the gastric wall.

The semi-isolated preparation, which consists of the gastric wall with the muscles, STG, OG and associated nerves, was employed to observe how motor nerves innervate identified muscles. Identification of the cardiac bursting units of the peripheral nerves was also made in this preparation: the son input fibers were stimulated by brief pulses with moderate intensity and frequency to activate rhythmic motor outputs from the STG. The semi-isolated preparation, including the CG, was used to study stimulus-induced cardiac motor activity. The son input fibers were activated by stimulation of the afferent fibers of a mandibular nerve which enter the CG.

The saline used here was modified from that for *Squilla* developed by Watanabe *et al.* [17]. It had the following composition (in mmol/l): Na, 450; K, 15; Ca, 10; Mg, 20; Cl, 525; N-2-hydroxyethylpiperazine-N′-2-ethanesulfonic acid (HEPES), 2. The saline was adjusted to pH 7.6. All experiments were done at room temperature (20–26°C).

RESULTS

Anatomy

Muscles The muscles of the cardiac stomach are shown diagrammatically in Figure 1A. Some of these muscles have been named by Kunze [15]. Some have not been previously identified, and are described later. All of these muscles are bilaterally symmetrical.

Four cardiac muscles are associated with medial movements of the dorsolateral gastric wall. The intrinsic longitudinal cardiac muscle 1 (lcm1) attaches to the dorsal gastric wall near the pcp and runs to the anterior region of the cardiac stomach. It serves to constrict the dorsolateral gastric wall. Two extrinsic muscles, which are antagonists of the lcm1, are the dorsal cardiac muscle (dcm) and the dorsolateral cardiac muscle 1 (dlcm1). The dcm originates on the dorsal carapace and inserts on the dorsal gastric wall. The dlcm1 originates on the lateral carapace and inserts on the dorsolateral gastric wall ventral to the lcm1. They dilate the gastric wall. The unpaired dorsal anterior cardiac muscle (dacm) is also an antagonist of the lcm1. The dacm originates on the anterior ventral carapace, and inserts on the anterior extremity of the cardiac stomach. Its contraction pulls the anterior gastric wall forward.

Six cardiac muscles are associated with medial movements of the lateral gastric wall which is medially folded to form the lateral cardiac fold (lcf). The intrinsic longitudinal muscles 2 and 3 (lcm2, lcm3) attach to the lcf. The lcm2 originates on the gastric wall at the lateral side of the pcp, and runs anteriorly. The lcm3 originates on the gastric wall at the ventral side of the pcp, and runs

anteriorly parallel to the lcm2. The lcm2 and lcm3 move the lateral gastric wall medially. The antagonists of the lcm2 and lcm3 are the dorsolateral cardiac muscles 1 and 2 (dlcm1, dlcm2), respectively. The extrinsic dlcm2 originates on the lateral carapace where the dlcm1 attaches, and inserts on the ventrolateral gastric wall. The lcm2 and lcm3 are situated between the dlcm1 and dlcm2. The intrinsic posterior cardiac muscle (pcm) attaches to the lateral gastric wall at the ventral side of the pcp. The pcm serves to constrict the posterior lateral gastric wall in front of the pcp. The posterior lateral cardiac muscle (plcm) originates on the posterior lateral carapace, and inserts on the lateral gastric wall near the pcp. The plcm is an antagonist of the pcm.

Kunze [15] has described dacm, dcm, dlcm, pcm and plcm but not lcm1, lcm2 and lcm3. Besides these identified cardiac muscles, 2 intrinsic and 5 extrinsic muscles insert on the ventral gastric wall (not shown).

Innervation The stomatogastric nervous system and peripheral motor nerves are illustrated in Figure 1B. Most of the nerves are bilaterally paired. The anterior ventricular nerve (avn) leaves the STG a short distance posteriorly, carrying motor axons to the dacm. The lateral ventricular nerve (lvn) leaves the anterior end of the STG, and runs posteriorly along the lcm1 on the gastric wall, branching extensively at the region just anterior to the pcp. The dorsal, median and ventral lvn (d-lvn, m-lvn, v-lvn) supplies motor nerves to the muscles of the pcp and pyloric stomach [16]. The posterior lateral nerve (pln) connects the lvn with the son emerging from the CG which resides on the circumoesophageal connective (coc).

The lvn and son divide peripherally into two functional groups of motor nerves: cardiac constrictor nerves (cn) and cardiac dilator nerves (dn). Two branches emerging from the lvn run dorsally to innervate the anterior and posterior dcm. These nerves are named the dn1 because they innervate the same muscle. The cn1 branches from the lvn anterior to the pcp to innervate the lcm1. The pln gives rise to several branches. The dn2 is a long branch, traveling anteriorly to innervate the dlcm1. The cn2 and cn3 are short branches carrying motor axons to the lcm2 and lcm3, respectively. The dn4 is a small branch which innervates the plcm. The son leaves the stomatogastric nerve (stn) posterior to the STG, and runs within the dlcm2, sending out the dn3 to it. The cn4 branches from the son near the pln to innervate the pcm.

The OG sends out several nerves. The ion connects the OG with the CG, and it branches extensively on the ventral gastric wall. These branches innervate intrinsic and extrinsic muscles which insert on the ventral gastric wall. They have not been examined in this study which is concerned with the motor activity of the STG relevant to the control of the muscles in the cardiac stomach.

Physiology

Cardiac cycle The dorsal and lateral gastric walls are moved by the sequential contractions of identified muscles. The patterned outputs that control movements of the cardiac stomach are provided by the motor axons which run in the avn, lvn and son. Recordings of spontaneous motor activity were made simultaneously from the lvn and son in semi-intact preparations. Movements of the cardiac stomach were observed by monitoring the motor activity. Spontaneous firing patterns of STG motor activity recorded from the lvn and son are shown in Figure 2. The cyclic motor outputs consisted of long-lasting bursts of alternately firing constrictor and dilator units (Fig. 2A). Bursts repeated at variable frequencies averaging about 5/min. The duration of bursts in the two units ranged from 3 to 15 sec. The impulse frequency in the constrictor units ranged from 30 to 120 Hz, and in the dilator units from 20 to 80 Hz. The initial units in the bursts leading to constriction of the gastric wall occurred simultaneously in the lvn and son. They were followed by dilator impulses. These patterned outputs are termed the cardiac cycle. There were variations of the motor activity of two units in these output nerves. In Figure 2B-D alternate silent periods in dilator and constrictor units are observed in the lvn or son. Such variations of the motor pattern seemed to be related to functional movements of the cardiac stomach (see later). Spontaneous cardiac cycles were rarely seen even in the semi-isolated preparation which included the CG and

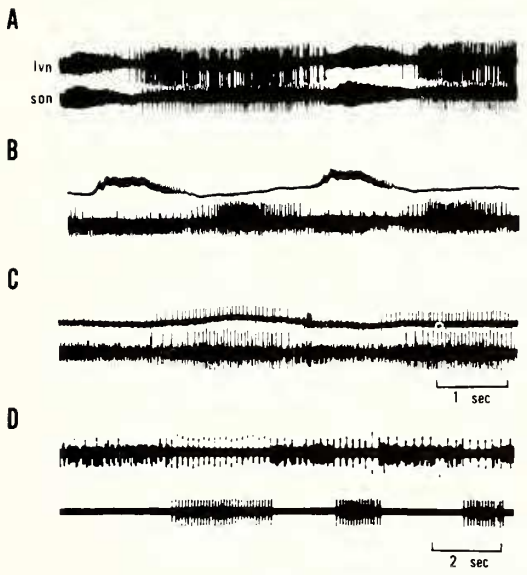

FIG. 2. Cyclic motor activity of the STG related to movements of the cardiac stomach. Spontaneous bursts were simultaneously recorded from the lvn and son. Initial bursts occurred in constrictor units, and were followed by those of dilator units. A: All constrictor and dilator burst units fired alternately. B–D: Either dilator or constrictor units were silent. In B and C displacements of the lvn trace are due to muscular contractions.

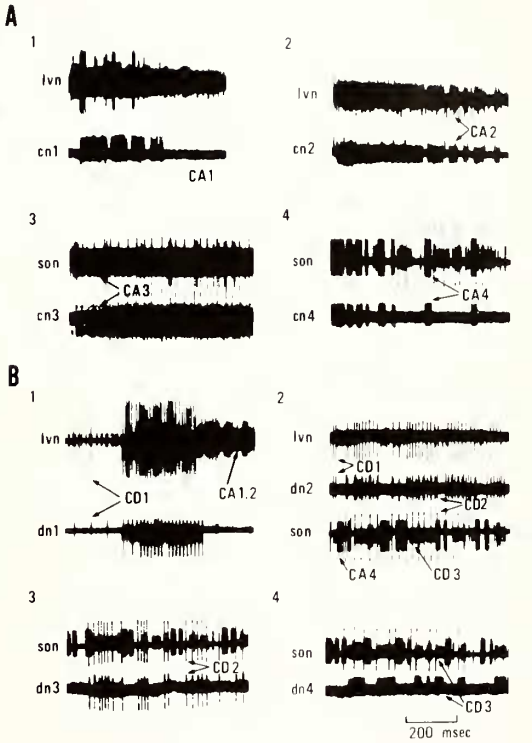

FIG. 3. Bursting units in peripheral nerves corresponding to those of the lvn or son. *En passant* recordings were made from the lvn or son at the region anterior to its ramification. The peripheral bursting units were recorded from nerve branches invading identified muscles. A: Burst firing of cardiac constrictor neurons (CA1–CA4). B: Burst firing of cardiac dilator neurons (CD1–CD3) (see text).

OG as well as the STG with associated nerves (similar to a combined preparation in the lobster: [1]). The avn was too small to permit monitoring impulses from it, but contraction of the dacm could be seen during bursting of dilator units.

The bursting pattern contributes to the sequential muscular contractions of the cardiac stomach. The burst units of the lvn and son observed by *en passant* recording correlate with those of their peripheral nerves invading various identified muscles. An example of such recordings is shown in Figure 3. The cardiac constrictor and dilator units are designated as CA and CD, respectively. The bursts of the lvn consist of two constrictor units. The bursting units of CA1 and CA2 are propagated to the cn1 and cn2, respectively (Fig. 3–A1, 2). Identification of these two units can be made by using the peripheral recording electrode for electrical stimulation of the axon to elicit an antidromic impulse in the lvn. The son also contains motor axons of two constrictor neurons. The long-lasting bursting unit of CA3 travels to the cn3 (Fig. 3–A3), and the short bursting unit of CA4 to the cn4 (Fig. 3–A4). The CA2 and CA3 neurons appear to discharge for a longer period than the CA1 and CA4 neurons. For the dilator units, the burst of large impulses in the lvn, which is attributed to CD1, is propagated to the dn1 (Fig. 3–B1). The dn2 contains two motor axons: one originates from the CD1 neuron, and the other from the CD2 neuron (Fig. 3–B2). Large impulses of CD2 unit in the son travel to the dn3 (Fig. 3–B3). The burst of small impulses of CD3 unit is propagated from the son to the dn4 (Fig. 3–B4). The size of impulses of the cardiac constrictor and dilator neurons extracellularly recorded from the lvn and son is relatively consistent: CD1 and CD2 are larger than CA, and CD3 is the smallest (Fig.

3–B1, 2).

The bursting patterns of motor outputs such as shown in Figure 2 are associated with movements of the cardiac stomach. The dorsolateral gastric wall is moved medially by contractions of the lcm1 and lcm2. The corresponding motor pattern is shown in Figure 2D. Two constrictor (CA1, CA2) and 2 dilator (CD1, CD2) neurons contribute to this movement. Medial movements of the posterior lateral gastric wall in front of the pcp arc commanded by the CA3 and CA4 neurons, each causing contractions of the lcm3 and pcm. The motor pattern is shown in Figure 2C. During these two types of movements, ingested foods may be moved backward or forward in the cardiac stomach. Besides these movements, the dorsolateral and posterior lateral gastric walls are moved medially. The motor patterns shown in Figure 2A and B control these movements. The CA1 and CA2 neurons command constriction of the dorsolateral gastric wall, while the CA3 and CA4 neurons command constrictions of the lateral and posterior lateral gastric walls. During sequences of all these types of movements, ingested foods would be macerated into fine particles. Other types of patterned motor outputs are shown in Figure 5. These output patterns may control the pumping of digestive juices or the transfer of digested food between the cardiac and pyloric stomachs (see later).

Table 1 summarizes the present observations on motor neurons, location of axon, muscles innervated and their functions. Although the precise number of neurons in the STG could not be determined, there seemed to be at least 7 motor neurons involved in the generation of the cardiac cycle.

Priming effect of input fibers via CG The son inputs induced dual effects on the motor activity of the STG: one input accelerated the pcp-pyloric cycle, and the other activated the cardiac cycle [16]. Cardiac cycles such as those seen during spontaneous activity (Fig. 1A) could be activated in the semi-isolated preparation by stimulating afferent fibers of the mandibular nerve with moderate intensity at 50 Hz, the highest frequency tested in this series of experiments (Fig. 4). Such stimulation activated the son input fibers via the CG. The pcp-pyloric cycle, which consisted of pyloric (PY) and pyloric dilator (PD) bursting units, repeated at a rate of about 2 Hz before stimulation. It disappeared gradually during stimulation, while the long-lasting cardiac cycle units were activated. The size of the PD and CD1 impulses is almost the same in this record. They can be distinguished by burst firing in the son which occurs simultaneously with the PD burst (see squares in Fig. 4). Initially, repetitive firing of the CD1 and CD2 neurons occurred in the lvn and son. It was followed by bursting of the CA1 and CA3 neurons. Bursting of the PY units in the lvn appeared to be accelerated during the high-frequency discharges of the CD1 neuron, and inhibited during the activity of the CA neurons

TABLE 1. Motor neurons of the cardiac cycle in the STG

Neuron		Location of axon	Muscle innervated	Function
Cardiac constrictor				constricts the gastric wall
	CA1	lvn, cn1	lcm1	
	CA2	lvn, cn2	lcm2	
	CA3	son, cn3	lcm3	
	CA4	son, cn4	pcm	
Cardiac dilator				dilates the gastric wall
	CD1	lvn, dn1 lvn, dn2	dcm dlcm1	
	CD2	son, dn2 son, dn3	dlcm1 dlcm2	
	CD3	son, dn4	plcm	

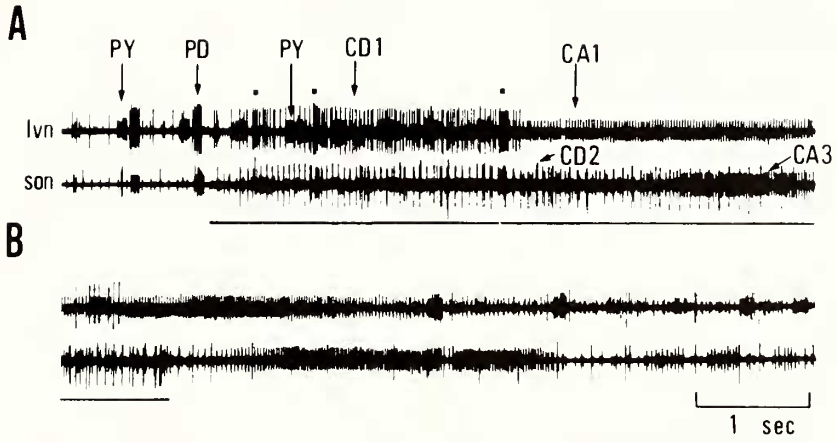

FIG. 4. Cardiac cycle triggered by son input fibers activated by repetitive stimulation of afferent fibers of the mandibular nerve entering the CG with moderate intensity at 50 Hz (marked by the underline). Records A–B are continuous recordings. A long-lasting cardiac cycle was activated during the stimulation. The CD1 and CD2 neurons fired initially, and thereafter the CA1 and CA3 neurons fired. PY, pyloric units: PD, pyloric dilator units. Bursts of PD occurred simultaneously with those in the son (see squares).

(Fig. 4A). Bursting of the CA neuron in the son was preceded by that in the lvn. Both continued after the cessation of stimulation (Fig. 4B). The priming effect was dependent on the stimulus frequency: the cardiac cycle became more obvious with increasing frequency. This observation suggests that some inputs from the CG may be necessary for activation of the cardiac cycle pattern generator.

Interaction of cardiac and pcp-pyloric cycles The function of the cardiac stomach is to macerate food and to transfer digested particles to the pyloric stomach. The pcp-pyloric cycle commands the opening and closing of the channels in the pcp and pyloric stomach [16]. Functional interactions between the cardiac and pcp-pyloric cycles were studied in the semi-isolated preparation. Modulation of the cardiac cycle by the pcp-pyloric cycle units was examined after cycling had been triggered by stimulation of son input fibers. An example is shown in Figure 5. Bursting of the CA1 and CA4 neurons was suppressed by bursting of the PY neurons (Fig. 5A, B). The CA and PY neurons fired alternately. The PY neurons provide the motor commands for movements of the ampulla in the pyloric stomach which forms the

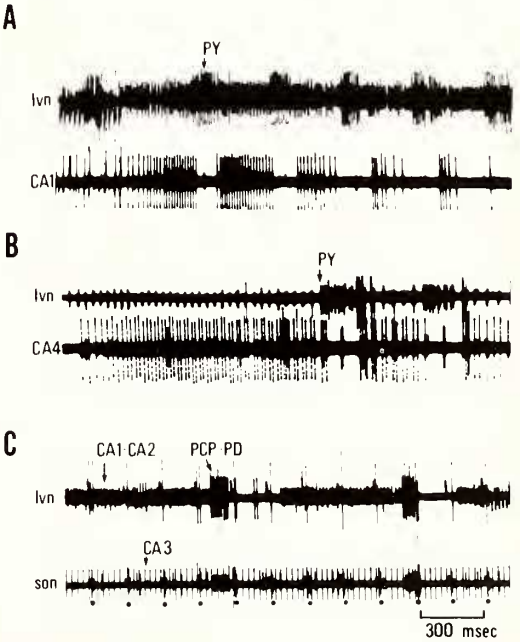

FIG. 5. Modulation of cardiac cycle units by pcp-pyloric cycle units. A, B: Bursts of CA1 and CA4 neurons were suppressed during bursting of PY neuron. C: Bursts of PCP and PD neurons suppressed bursting of CA1 and CA2 neurons. Bursting of CA3 neuron continued during bursting of PCP and PD neurons. Dots indicate individual stimuli given to the son.

channels leading to the midgut [16]. The CA1 and CA4 neurons control contractions of the lcm1 and pcm, respectively. The results, therefore, indicate that constrictions of the dorsolateral and posterior lateral gastric walls near the pcp may not be occurring during constriction of the ampulla. In Figure 5C bursting of the CA1 and CA2 neurons recorded from the lvn was suppressed by that of the pcp neurons 1 and 2 (PCP1, PCP2) and PD neurons in the pcp-pyloric cycle. The PCP and PD neurons provide the motor commands for opening the pcp and cardio-pyloric channels. Bursting of the CA3 neuron, as recorded from the son, continued without inhibition from the PCP and PD neurons. The observations suggest that the CA neurons, which command constriction of the dorsolateral gastric wall of the cardiac stomach, may be inactivated during the opening of the pcp and pyloric channels to allow the transfer of suspensions of food particles from the cardiac to the pyloric stomach.

DISCUSSION

The stomatogastric nervous system in decapods has been widely used for research on the generation of rhythmic motor output pattern [1, 2]. We have introduced the stomatopod preparation, which lacks the gastric system found in the STG of decapods, to comparative neurophysiology of this nervous system [16]. In the previous paper, the pcp-pyloric system of *Squilla* was analyzed for comparison with the pyloric system in decapods, *Panulirus* and *Homarus*. In the present paper, the anatomy and physiology of the cardiac system in the STG of *Squilla* has been described. The cardiac ossicles located on the cardiac sac are not a chewing system like gastric mill ossicles in decapods [14, 15]. The food, partially masticated by the mandibles, is macerated by muscular contractions of the cardiac stomach with the aid of digestive juices that are pumped forward by the pcp and pyloric stomach [15, 16]. Four intrinsic muscles and 5 extrinsic cardiac muscles that constrict or dilate the dorsal and lateral gastric walls have been identified. All of these identified muscles are innervated by motor axons from the constrictor and dilator neurons in the STG.

Innervation

It is of interest to compare innervation of the muscles in the cardiac stomachs of stomatopods and decapods. Maynard and Dando [5] have described the detailed anatomy of muscles and nerves of the stomach in several decapods. In *Squilla* the lvn is the principal nerve carrying the motor axons which innervate the muscles of the pcp and pyloric stomach [16]. It was found that the lvn and, in addition, son are the principal nerves which contain motor axons both of the cardiac constrictor and dilator neurons of the STG. They divide peripherally into constrictor and dilator nerves supplying 8 identified muscles. One extrinsic muscle is doubly innervated. In *Panulirus*, on the other hand, the dorsal ventricular nerve contains most of motor axons from the STG which innervate the muscles of the gastric mill and pyloric stomach [1]. The anterior median nerve and median ventricular nerve (mvn) carry the motor axons of the cardiac constrictor neurons (AM and IC neurons) of the STG which innervate the muscles of the cardiac stomach and the muscles of the ventral cardiac ossicles (cv2) [1, 5, 11]. The motor innervation provided by the cardiac constrictor neurons in *Panulirus* is relatively simple, and differs from that in *Squilla*. In *Panulirus*, the mvn also contains a motor axon from the cardiac dilator neuron (VD neuron) which innervates the muscles of the ventral cardiac ossicles (cv1). The cv1 and cv2 muscles move the ventral gastric wall of the cardiac stomach in *Panulirus*: the one is homologous to the plcm in *Squilla*, and the other to the pcm. Four nerves carry motor axons of 2 cardiac dilator neurons (CD neurons) in *Panulirus* [11, 12]. Motor nerves branch from these nerves to innervate 7 extrinsic muscles: 5 muscles are innervated by the CD1, 4 muscles by the CD2, and thus 2 muscles receive a double innervation. The peripheral courses of the CD neurons in *Panulirus* appear complex compared to those in *Squilla*.

Cardiac cycle

Cardiac cycling occurred spontaneously in STG of semi-intact preparations (Fig. 2). The most notable characteristics of the cardiac cycle pattern, compared to the pcp-pyloric cycle pattern, are that

the burst duration is very long (over 10 times), the cycle rate is low, and the pattern is composed of only two alternately bursting groups. Although cardiac cycles did not occur spontaneously in the semi-isolated preparation, they could be produced by activation of the son inputs. These were activated via the CG by stimulation of afferent fibers (Fig. 4).

While the cardiac cycle is brought on by inputs from a higher center, the pcp-pyloric cycle is intrinsic to the STG, although it is modifiable [16]. The mechanism of cyclic pattern generation may be different for the two cycles. The cardiac cycle is generated by two groups of neurons. Four CA neurons and 3 CD neurons could be identified in the STG from the peripheral recordings (Fig. 3), but interactions present among them were not analyzed.

Comparison with the motor neurons of the cardiac system between stomatopods and decapods has been made as follows. In *Panulirus,* they have been described by Moulins and Vedel [11]. The CA1, CA2 and CA3 neurons are homologous to the AM neuron in *Panulirus.* These neurons control movements of the intrinsic muscles spread over the gastric wall. The CA4 neuron may be functionally homologous to the IC neuron in *Panulirus.* Both command constriction of the posterior lateral gastric wall. The CD3 neuron may be homologous to the VD neuron in *Panulirus*: the one is an antagonist of the CA4 neuron, and the other of the IC neuron. The VD and IC neurons are involved in the pyloric cycle [7]. The function of these neurons appears to be related to movements of both the cardiac and the pyloric stomachs, although their role in the pyloric cycle is unknown [6, 11]. Comparison of the phase relationships of the pcp-pyloric cycle in *Squilla* with those of the pyloric cycle in *Panulirus* suggests that the PCP1 (or PCP2) and PCP3 neurons, which control cardiac plate muscles, are homologous to the VD and IC neurons, respectively [16]. It is unknown whether the CA4 and CD3 neurons are involved in the pcp-pyloric cycle in controlling movements of these muscles. The CD1 and CD2 neurons in *Squilla* are certainly homologous to those in *Panulirus.* The two CD neurons in *Panulirus* exhibit complex functional properties that contribute to the organization of the neural network taking part in motor commands [11, 12]. The cell body of CD1 is located in the OG, and that of CD2 in the STG. Furthermore, their peripheral nerve distributions are quite complex. Such complexity has not been observed in the 3 CD neurons of *Squilla.* Their cell bodies are located in the STG.

The functional movements of the cardiac stomach commanded by the cardiac cycle can now be described, although movements of the ventral gastric wall remain to be analyzed. Three of the four types of movements of the gastric wall described by Kunze [15] have been examined in this study. Four variations of spontaneous cardiac cycling are associated with them. The motor patterns shown in Figure 2D command medial movements of the dorsal and lateral gastric walls (termed the first phase by Kunze). The motor patterns which contribute to medial movements of the dorsal, lateral and posterior lateral gastric walls (the second phase) are illustrated in Figure 2A, B and C. Medial movements of the anterior dorsal gastric wall (the third phase) appear to be commanded by the motor pattern similar to that shown in Figure 2D, because the constrictor neurons in the son do not fire in this pattern. Maceration of ingested food may occur during these three phases while the pcp lateral channels are closed. Kunze [15] has seen the fourth phase which seems to occur sporadically. During this phase, digested food are transferred by simultaneous muscular contractions from the cardiac to the pyloric stomach through the pcp lateral and cardio-pyloric channels. Such food movements have not been examined in this study (see next section).

Functional relations between cardiac and pcp-pyloric cycles

It has been shown that once the cardiac cycle is activated by stimulation of the son input fibers, the pcp-pyloric cycle is suppressed [16]. On the other hand, it was found that the pcp-pyloric cycle units suppressed the cardiac cycle units: the PY neurons inhibited the CA1 and CA4 neurons (Fig. 5A, B); the PCP1, PCP2 and PD neurons also inhibited the CA1 and CA2 neurons (Fig. 5C). In both cycles

the units fired alternately. The CA1 and CA4 neurons control contractions of the lcm1 and pcm, respectively, to bring the dorsolateral gastric wall medially in front of the pcp. Thus, the gastric wall can be tightly pressed to the dorsal floor of the pcp, resulting in blockade of the cardio-pyloric channel. The PY neurons command constrictions of the ampulla in the pyloric stomach, which cause a backflow of digestive juices to the cardiac stomach through the cardio-pyloric channel from the pyloric ampullary channels [15]. The inhibition of the cardiac constrictor neurons by the pyloric neurons probably makes the backflow possible. Figure 5C shows the pattern of motor outputs likely to represent the commencement of the transfer of digested food from the cardiac to the pyloric stomach: the CA neurons command constrictions of the gastric wall to force food suspensions backward, and the PCP and PD neurons command the opening of the pcp lateral and cardio-pyloric channels. In *Panulirus*, the CD neurons accelerate or inhibit the PD neurons [11]. Such modulation of the pcp-pyloric cycle by the cardiac cycle units appeared to be present in the *Squilla* STG (Fig. 4). However, the functional significance of such modulation is still unknown.

The present study has shown that the cardiac cycle of the STG in *Squilla*, as well as the pcp-pyloric cycle, is of special interest for studying the characteristics of central pattern generators. Differences between the two cycles have been described. The cardiac and pcp-pyloric systems also provide useful models for understanding the mechanism underlying the generation of rhythmic motor patterns. The cellular properties and neural networks of the two subsystems of the STG in stomatopods will be studied for comparison with those in decapods which have been well analyzed.

ACKNOWLEDGMENTS

The author is grateful to I. M. Cooke, J. A. Benson and M. W. Miller for critical review and suggestions on this manuscript; H. Fukuyama and M. Funahashi for technical assistance; to R. Miyamoto for illustrations. This work was supported in part by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture of Japan (No. 59540460).

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